BEHAVIOUR OF CRUSTACEA: ECOLOGICAL AND SOCIAL PERSPECTIVES

SANDRA L. GILCHRIST

Visual, chemical, acoustical, and tactile information can vary crustacean responses to social and ecological conditions. The relative importance of the types of cues received can vary in marine, semi-terrestrial, and terrestrial environments. Some species experience only one of these types of habitats throughout their lifetimes while other species encounter all three habitats during particular life stages. Variations of ecological parameters within habitat lend specific context to actions and reactions exhibited by decapods. Population dynamics and social behaviour of decapod crustaceans are reveiwed with reference to how age structure and ecological conditions influence perception of environmental and social signals. Of particular interest are cues which relate to development of space use, home range, territoriality and food gathering relative to potentially limiting abiotic and biotic resources. As model systems, specific case analyses will be made for hermit crabs and tree crabs. ☐ *Crustacea, behaviour, age, structure.*

Sandra L. Gilchrist, Division of Natural Sciences, New College of USF, Sarasota, FL USA; 6 July, 1990.

Successful invasion of terrestrial habitats by crustaceans is limited to relatively few species scattered among a small number of taxa. Only one semiterrestrial shrimp *Merguia* has been described (Abele, 1970; Bliss, 1968; Gilchrist *et al.*, 1983); however, little is known of its behaviour or physiology. Many land crabs spend a large amount of time in terrestrial habitats, although most still require an aquatic medium for reproduction (see Burggren and McMahon, 1988 for a discussion of terrestrialisation). Terrestrial species have some obvious external variations which differ from aquatic counterparts in respiratory apparatuses and in appendages (especially appendages used in arboreal movement). Behavioural modifications are much more common in crabs existing in terrestrial environments than in aquatic environments, especially relative to locomotion, communication, feeding, mating, gas exchange and osmoregulation. Development of offspring also tends to be more abbreviated as crustaceans become more terrestrialised (*Merguia*; Abele, 1970; Burggren and McMahon, 1988).

Age structure of the various populations also differs. For example, in terrestrial species juveniles rarely are encountered among adults; while in aquatic species, there may be a wide size range of individuals occupying a single habitat. Cannibalism has been noted commonly among some land crabs and may maximise distribution of food materials acquired during larval stages while reducing reproductive cost of consuming one's own offspring broadcast into an aquatic environment through supplying materials to sibling survivors (Wolcott, 1988; Helfman, 1979). While potential cannibalism may explain some age class distribution patterns, ecological factors such as environmental stress and predation by non-conspecifics are also important. There are differences in behaviour between aquatic and terrestrial juveniles as well as striking variations between juvenile and adult conspecifics associated with physiological constraints and predation. However, differences between behaviours of the aquatic and terrestrial species seem to appear after emergence onto land.

An exhaustive review of behavioural variations inter- and intraspecifically for aquatic and terrestrial crabs is beyond the scope of this analysis. Rebach and Dunham (1983) edited an excellent series of papers dealing with various aspects of behaviour. In this study, I will expand on some of the topics discussed in their series relative to age structure and ecological context.

To illustrate behavioural alterations relative to age structure and ecological conditions, I will limit this discussion to selected representatives of the Anomura (*Birgus, Calcinus, Clibanarius, Coenobita,* and *Pagurus*) and Grapsidae (*Aratus*). These genera show varying degrees of sociality as well as a range of terrestrialisation.

AGE STRUCTURE

The literature is replete with examples of com-

mon occurrences of adult and juvenile crabs in aquatic habitats.

Groups may gather for many reasons, for example exploitation of a common resource such as observed at areas where gastropod shells are released by predators (Gilchrist, 1982; McLean, 1974; Rittschof, 1980) and feeding sites (Scully, 1983) or aggregation to relieve environmental stress (such as shading or trickle cooling).

Aquatic hermit crabs gathering in areas where gastropods are consumed (termed predation sites) are of a wide size range even at a single site (Gilchrist, 1982; Rittschof, 1980). Typically, crabs form in a semicircular pattern downstream of the predation site with larger, interactive crabs near the front of the group and smaller crabs near the rear. Shell exchanges are common and rapid at natural sites (Gilchrist, 1982; Rittschof, 1980), some mating occurs, and in less than 1% of observations cannibalism on a smaller crab takes place. Active physical interactions are common as the crabs establish a dominance hierarchy at such sites. In shell exchange experiments conducted in the field and the laboratory, rarely is mortality among opponents recorded (major works record no mortality: Abrams, 1981; Hazlett, 1989; Imafuku, 1989). For the terrestrial hermit crab *Coenobita compressus*, newly metamorphosed juveniles seeking shells do respond to simulated predation sites (crushed gastropods; Table 1) in association with more aquatic species. Preliminary light microscope observations suggest that as the land hermits animals molt and emerge onto land, setation patterns on the appendages alter, becoming less dense and appearing shorter. Ghiradella *et al.* (1968) indicated that aesthetascs of *Coenobita* resemble chemoreceptors of terrestrial insects. Adult *Coenobita compressus* do not appear differentially attracted to crushed gastropods in greater numbers than to other carrion. Rittschof and Sutherland (1986) noted that chemical cues stimulated feeding behaviour of *Coenobita rugosus*, but did not seem important in eliciting shell seeking behaviour. Electron micrographic analyses of the setae and receptors may reveal differences in morphology and function of these structures ontogenetically with the transition from aquatic to terrestrial habitats. It is interesting to note, however, that some intertidal hermit crabs observed in the tropics do not appear to respond to predation sites (Table 2) as frequently as more temperate counterparts. Clearly, they can respond to certain gastropod fleshes, however, it is not obvious whether nonresponse to other fleshes is control-

TABLE 1. Responses of newly metamporphosed *Coenobita compressus* to simulated predation sites using G statistic with 1 df after correction for continuity.

Flesh type	Respondents		
	control*	treatment	significant
Acanthina brevidentata	2	101	++
Thais melones	3	14	
Nerita scabricosta	1	61	+
Cerithium stercusmuscarum	4	36	+
Anachis varia	7	58	+
Anachis fluctuata	3	30	+
Anachis rugosa	4	8	
Nassarius exilis	1	73	++
Mitra tristis	1	11	
Cantharus elegans	0	142	++
Turbonilla panamensis	1	18	
Siphonaria gigas	3	9	
Siphonaria maura	1	15	
Conus brunneus	5	11	
Littorina aspera	0	137	++

* Cage w/shell alone

led behaviourally or at the receptor level. The mean size (hard carapace length) of crabs attending flesh sites was 7.02 mm± 1.65, indicating that for these experiments only medium to large crabs were attracted to gastropod fleshes. After a period of time (6–8 hours) hermit crabs in the experiment came to the flesh sites and consumed the gastropods. These crabs, like aquatic counterparts (Lepore and Gilchrist, 1988) may be attracted by degradation products such as putrecine and cadaverine.

As terrestrialisation increases, physiological and physical constraints tend to separate activities of different age groups both temporally and spatially. Herreid and Full (1986) observed that large *Coenobita compressus* travel faster than smaller crabs, doubling speed as leg length doubles. They also observed that smaller crabs expend more energy walking and climbing relative to balancing the shell. Thus, it would be expected that smaller crabs which may be more subject to predation and dessication would move smaller distances from refugia. Adult crabs tagged in Panama moved several hundred metres a day while smaller crabs tended to make short forays from the jungle edge to the wrack line for feeding. When climbing, large crabs fell less frequently than small ones.

Adult *Birgus* are large and somewhat solitary. Aggregations may be observed around a food source (Grubb, 1971) although burrows and rock

TABLE 2. Relative attraction to gastropod flesh by *Calcinus obscurus* in intertidal and subtidal areas of Panama. Gastropods were crushed and placed beneath cages while controls were cages alone and a cage plus a shell (controls were not significantly different, thus were pooled in the analysis). Null hypothesis that responses were independent of flesh was tested using G Statistic with 1 df after correction for continuity.

Gastropod flesh	Intertidal				Subtidal		
	Culebra	Flamenco	Naos	Taboga	Taboga	Uva	Perlas
Cantharus ringens	NS	NS	NS	NS	+	NS	NS
Cerithium stercusmuscarum	NS	.	.	+	+	+	+
Planaxis planicostata	NS	NS	NS	+	+	+	+
Anachis fluctuata	NS	NS	NS	NS	NS	NS	NS
Nerita funiculata	NS	NS	NS	NS	NS	NS	NS
Thais melones	NS	NS	NS	NS	NS	NS	NS

shelters (resting sites) are typically occupied singly. Very small individuals are not recorded co-occurring with adults (Gilbson-Hill, 1947). Much of the work with physiological parameters of *Birgus* has been done with smaller specimens (<500g; McMahon and Burggren, 1981; Morris, Greenaway and McMahon, 1988). Thus a full comparison of segregation by environmental stress is not yet practical.

Aratus, like *Birgus*, are rarely observed in groups of mixed size ranges. Within the canopy and on mangrove trunks at study sites in Sarasota and Manatee Counties in Florida, crabs with carapace widths less than 10mm were observed infrequently (Fig. 1). When a larger crab encounters a smaller one on the trunk, typically the smaller crab moves to the opposite side of the trunk. In over 50 hours of field observations, only 2 instances of conspecific predation were observed. Such predation occurred in the laboratory primarily after one crab molted, even when conditions were crowded. Beever *et al.* (1979) and Burton (1990) did not record conspecific predation. However, one of the most voracious predators of adult *Aratus* is another crustacean, *Goniopsis cruentata*. Warner (1967) describes a specific response of this predator to *Aratus*. Other invertebrate predators for adults include *Callinectes* and *Eurytium*. Birds, skunks, raccoons, and fish have been observed consuming adults. Juveniles appear to be eaten primarily by *Callinectes* and by birds (pers. obs.). *Callinectes* propel themselves up out of the water at high tide and either grab *Aratus* or knock them from the

mangrove roots into the water. *Aratus* adults jump either somersaulting backwards or forwards from one horizontal surface to another when threatened by a predator. This action has been described to some extent by Ferris (1988). The crab can also leap from a lower surface to a higher one (pers. obs.). In a series of experiments where crabs were startled in the field (Table 3), larger crabs were more successful at landing or at reaching a greater height. When hanging upside down, the fourth pereiopods are used primarily in stabilizing the animal. In 2 cases where chelae were missing, animals had difficulties in making successful lands but did not fall when hanging upside down. Ferris (1988) described how these crabs right themselves when they land too far forward or upon their backs. Smaller
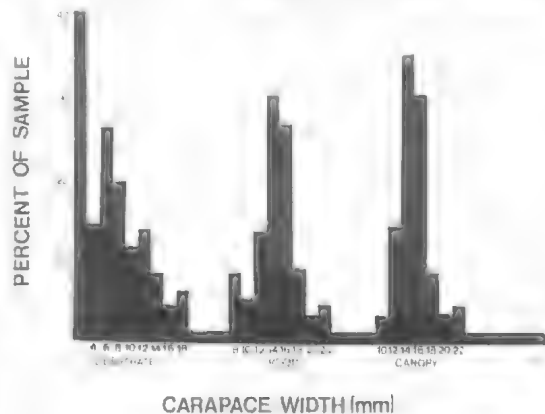

CARAPACE WIDTH (mm)

FIG. 1. Size distribution of *Aratus pisonii* on *Rhizophora mangle* at Tidy Island (Bradenton), Florida.

TABLE 3. Startle reaction of *Aratus pisonii* on roots and trunks of the red mangrove *Rhizophora mangle* at South Lido Beach in Sarasota Florida. Crabs were startled on roots by thrusting a dead *Callinectes sapidus* suspended by a thick metal rod at the crabs. On the trunk, a stuffed toy was used in a similar fashion.

	# of crabs	type of movement			relative size (carapace width in mm)	comments
		jump	horizontal	around		
roots	35	11	7	17	< 5	3 crabs which jumped made a successful landing; none jumped to a higher level — all jumped to lower level (water or lower root); most simply moved to the opposite side of the root.
	18	14	3	1	> 7	11 crabs jumped with 8 making successful landings — 6 jumped from higher to lower position and 2 jumped upward.
trunk	9	0	-	9	< 5	All crabs moved to the opposite side of the trunk and moved vertically downward.
	27	19	3	5	> 7	Most of the crabs jumped to a lower surface. When observing racoons, a predator in the area, those animals which simply move around the trunk or horizontally are captured and eaten with a high frequency. Bird predators were observed amputaing a leg as the crabs flung their bodies from the attackers.

crabs have a more difficult time in righting possibly because of the lack of experience or physical ability to do so effectively.

Wilson (1985) demonstrated that smaller *Aratus* are less tolerant of desiccation stress. Larger crabs which occupy canopy areas (temperature higher and relative humidity lower) are more tolerant physiologically and have developed behaviours (periodic dunking at high tide) which replenish water supply to the body. Thus, contact between various size classes is diminished.

Tidal clustering of crabs of mixed sizes (Fig. 2) as well as of mixed species has been observed for several intertidal species of hermit crabs (Gherardi and Vannini, 1989; Hazlett, 1966; Snyder-Conn, 1980, 1981). Such collections may aid in information exchange, shell distribution, mating, and resistance to desiccation, although exact mechanisms of the resistance are not yet fully understood. Although there is some disagreement (Gherardi and Vannini, 1989), such clustering seems to be effective in reducing desiccation. In experiments with *Clibanarus albidigitus* there were high losses of shell water in clustering crabs, however, the salinity of the shell water did not increase more than two parts per thousand (Table 4). This indicates that the shell water was probably not simply evaporating within the shell with time. The central bottom region of the cluster was cooler (2–4°C) than the surface of the cluster and the surrounding area. Perhaps by trickling water from the shells, the hermit crabs cooled the cluster by evaporation.

Land hermit crabs (*Coenobita clypeatus* and

C. compressus, C. perlatus and *C. rugosus*) of different sizes will aggregate under fallen logs, in shallow leaf burrows, and beneath manmade structures, i.e. beneath houses and water troughs. There is some movement in such aggregates, with one instance of copulatory behaviour observed (pers. obs.). No shell exchanges have been noted in more than 75 hours of monitoring such aggregates of *Coenobita compressus* in Panama. As the aggregate forms, it is interesting to note that chirping sounds are heard often,
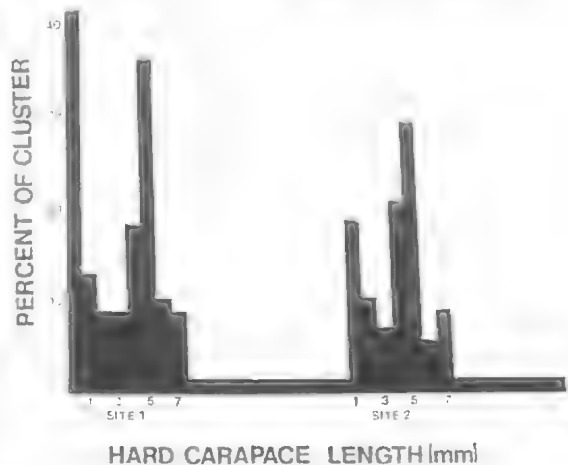

HARD CARAPACE LENGTH (mm)

FIG. 2. Size distribution of crabs (*Clibanarius albidigitus*) found clustering on rock marl benches in Pacific Panama. Site 1 is closest to the water's edge and site 5 is 20 meters shoreward and elevated 1 meter from site 1. Five clusters were examined at each site.

TABLE 4. Clustering of *Clibanarius albidigitus* on rock marl benches in Pacific Panama. Shell water extracted using tuberculin syringe from 50 shells chosen at random in 15 separate clusters. (Salinity measured using a refractometer, did not vary more than 2ppt during observation).

Site#	#clusters	x̄ number crabs cluster ± sd	x̄ cluster height ± sd	x̄ shell water/crab at cluster beginning ± sd	x̄ shell water crab after 3 hours ± sd
1	37	214 ± 39	4.2cm ± 1.6	.31cc ± .11	13cc ± .12
2	52	157 ± 50	4.0cm ± 1.3	.35cc ± .16	17cc ± .11
3	46	174 ± 31	3.3cm ± 1.2	.29cc ± .13	.06cc ± .13
4	29	116 ± 40	2.3cm ± 1.1	.34cc ± .16	.04cc ± .16
5	16	72 ± 16	1.8cm ± 0.7	.26cc ± .11	.11cc ± .08

*Increase in site number indicates movement shoreward of 5 metres. Sites 5 and 6 were 1 metre higher than other sites.

Accompanying the chirping sounds are rapid asynchronous flicking motions of the antennae. The intensity of these sounds appears to decrease as movement within the aggregate decreases. Grubb (1971) noted that *Birgus*, a relatively solitary hermit crab, continuously produces a clicking sound. The chordotonal organ in the antennal flagellum of *Petrochirus californiensis* (Taylor, 1967a, b) is thought to be sensitive to acoustic stimuli. However, such sensitivity has not been explored in the Coenobitidae. Although it is not clear what information is conveyed by the chirping, other accounts of sound production by land hermit crabs suggest that touch may also stimulate the behaviour (Imafuku and Ikeda, 1990). Some shell rapping and flicking with chelae occurred within *C. compressus* aggregations. In observations of the same aggregation site on 4 consecutive days, approximately 63% of the crabs were found returning all 4 days, suggesting some recognition or homing ability.

Page and Willison (1982) report broad overlaps of crab size ranges with variations in activity and distribution associated with the need for smaller crabs to replenish shell water more often and with rigid osmoregulatory requirements of small individuals. Land hermit crabs (*Coenobita clypeatus*) also may be found feeding and drinking in groups of mixed sizes, however, the time of greatest abundance varies somewhat (pers. obs.). These differences may be related to predation and physiological stress (Gilchrist, unpubl.), however, variability in 'safe sites' may cause wide fluctuations in observation (Geritz *et al.*, 1988).

SOCIAL BEHAVIOUR

Spatio-temporal variability in the environment requires that crustaceans adjust behaviourally to function efficiently. If social behaviour is an adjustment to the environment, then selection on these behaviours should occur (Seiple and Salmon, 1982). Social behaviours of crustaceans rarely exist as a single action pattern performed within a narrow intensity range; thus, plasticity of such behaviours is apparent.

Much of the work dealing with hermit crabs relates to the gastropod shell or other covering (Taylor *et al.*, 1989). More than 90% of non-taxonomic articles dealing with hermit crabs address shell or shell related phenomena. Reese (1963), Hazlett (1966), and Hazlett and Estabrook (1974) provided the basis for establishing a catalogue of behaviours observed during social interactions for several pagurids and diogenids. Acoustical displays are not included in the listing.

A brief review of shell use is important to understanding social interactions relating to this resource. Shell selection and use by hermit crabs are determined by a number of physical parameters of the shell as well as the motivation of the crab (Abrams, 1978; Dowds and Elwood, 1983, 1985; Hazlett, 1978, 1983; Kinosita and Okajima, 1968; Taylor, 1981). For adults, the shell may afford some protection but may also influence reproduction. As pointed out by Scully (1983) the relation between resource use and reproductive success is often assumed *a priori* to be correlated with fitness. Many authors have explored the influence of shell size on clutch size (Bertness, 1981; Childress, 1972; DeWilde, 1973; Fotheringham, 1980; Hazlett, 1989; Hazlett and Baron, 1989), although most major studies do not persist in observing hatch rate of eggs, recruitment into populations, and the influence of shell use on recruitment. For hermit crabs of several species observed in the laboratory the hatch rate was between 68 and 89% (Table 5) and survivorship through the glaucathoe molt was variable between species. In shell addition

TABLE 5. Laboratory observations of hatch rate for *Pagurus impressus*, *P. longicarpus*, and *P. maclaughlinae* using two methods of counting. For one data set, gravid females were weighed when captured and then again after larvae were liberated. Any eggs left on the pleopods and in the shell after 2 hours from hatching of last larvae were weighed and observed for development. The second method involved removing females from their shells, counting an aliquot of eggs, estimating egg number from the count, allowing females to re-enter a shell and then proceeding to count unhatched eggs two hours after liberation of larvae. Larvae were drawn to the surface by a strong light source and removed from the hatching tank.

Crab species	hatch rate				% surviving through glaucathoe	
	n	weighing	n	counting	weighing	counting
Pagurus impressus	20	68%	17	73%	0.1%	0.1%
Pagurus longicarpus	18	81%	17	83%	0.003%	0.002%
Pagurus maclaughlinae	23	83%	20	89%	1.1%	1.7%

experiments (Reese, 1963; Spight, 1977) some increase in population size is noted, however, I suggest that this apparent increase occurs from increased visibility of previously cryptic crabs. In a long term study of shell addition (>350,000 added to site in three years), populations of three species seemed to decrease while one species (*P. pollicaris*) increased only after two full years of shell addition (Fig. 3), added shells were assimilated into the populations. From these data alone, conclusions relating to shell use and recruitment over a long period of time seem uncertain. However, factors independent of shell use or shell availability may be used to explain the observed patterns. In 1985 and 1986 a series of strong storms occurred in the sampling area during the primary breeding season for the crabs. Few gravid females were collected, suggesting that recruitment might be low during the next 6 months. In 1987, *P. pollicaris* was collected in relatively high numbers during April and May but then decreased to near normal levels in June and July. During June and July stingrays moved into the area. Rays were observed harvesting the small hermit crabs in sandflat areas.

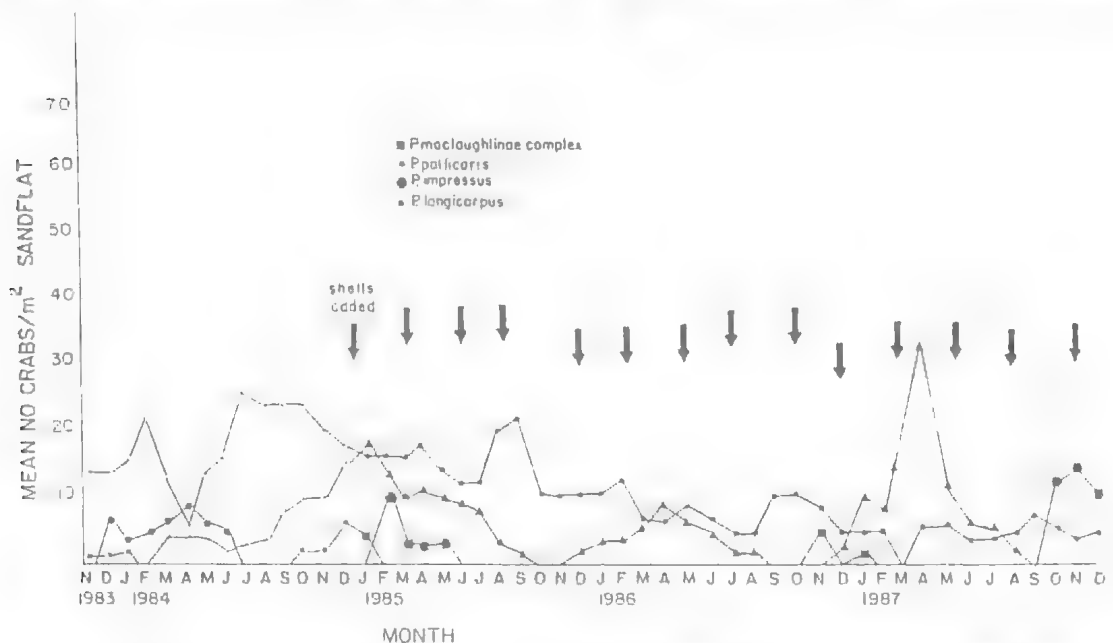Aggressive behaviour of female hermit crabs

FIG. 3. Long term shell addition experiment to observe effects of available shells on recruitment. Shell additions did not significantly alter long term population patterns.

TABLE 6. Water retention of shells and hermit crab desiccation relative to shell condition for *Coenobita compressus* in Pacific Panama.

Shell type	shell condition	crab size	n	$\bar{x} \pm$ sd amount of water retained (cc) after 1 hour full exposure	$\bar{x} \pm$ sd time[*] to crab extension from shell (min)
Nerita scabricosta	with algae	< 5mm	20	–	21 ± 6
	without algae	< 5mm	20	–	15 ± 7
	hole in apex	< 5mm	20	–	13 ± 5
	with algae	> 5mm	20	–	37 ± 4
	without algae	> 5mm	20	-	24 ± 4
	hole in apex	> 5mm	20	-	19 ± 6
Turbo saxosus	with algae[**]	< 5mm	20	–	31 ± 5
	without algae	< 5mm	20	–	20 ± 6
	hole in apex	< 5mm	20	–	15 ± 4
	with algae	> 5mm	20	$.31 \pm .11$	50 ± 9
	without algae	> 5mm	20	$.19 \pm .08$	41 ± 6
	hole in apex	> 5mm	20	$.06 \pm .04$	39 ± 14
Thais melones	with algae	< 5mm	20	$.38 \pm .14$	64 ± 15
	without algae	< 5mm	20	$.31 \pm .08$	51 ± 11
	hole in apex	< 5mm	20	–	30 ± 19
	with algae	> 5mm	20	$.52 \pm .17$	81 ± 8
	without algae	> 5mm	20	$.48 \pm .14$	74 ± 11
	hole in apex	> 5mm	20	$.21 \pm .11$	39 ± 14

[*] it was observed that prior to death crabs extended from shells and did not retract upon stimulation of abdomen; crabs reaching this point were quickly rehydrated.

[**] shell had only sparse amounts of algae observable from aperture.

does appear to alter during brooding. Neil and Elwood (1985) observed that gravid crabs (*P. bernhardus*) have decreased levels of attack and increased levels of defensive behaviour. They also note that shell exchange is infrequent. Gilchrist (1982) found that for *Clibanarius vittatus*, *P. pollicaris*, and *P. maclaughlinae* gravid females were more likely to have greater numbers of shell co-inhabitants than males. Hazlett (1970) suggest a chemotactile discriminatory cue while Imafuku (1986) postulated that receptive females may emit a water-borne chemical which facilitates discrimination between the sexes. It is not unreasonable to speculate that other organisms might use such chemicals to orient to a female as well. Further, these shell occupants were observed eating eggs as well as abdomenal appendages of the crabs. Gilchrist (1982) and Bertness (1981) observed that gravid crabs changed shells more often than nongravid ones, contradicting the observations made by Neil and Elwood. Perhaps this difference may be explained by variations in shell co-inhabitants in the various study areas. Current observations of *P. longicarpus*, *P. maclaughlinae* and *P. pollicaris* in Sarasota Bay (unpubl. data) indicate that gravid females of these species change shells

often, move into less saline waters for extended periods, and tend to be somewhat restricted in overall movement patterns.

Despite some evidence to the contrary (Gilchrist, 1982; Gilchrist and Abele, 1984; Wilber and Herrnkind, 1982), it is commonly assumed that hermit crab populations are limited by supplies of empty shells (Hazlett, 1981; Kellogg, 1976; Vance, 1972). Thus, many studies of interactions have focused on competition for this limiting resource. Consumption rate and combined effects of different sorts of variability (Chesson, 1985) are important in determining coexistence in specific natural systems. Superimposed on variation in consumption rate is the age structure pattern of the populations in that differences in shell use occur with crab age (Abrams, 1980).

Correlations have been noted between shell selection and level of environmental stress (Bertness, 1981c; Taylor, 1981, 1982; Young, 1980) as well as predation (Bertness, 1981c; Borjesson and Szelistowski, 1989).

Mortality of all life stages can result from predation (including parasitism). The type and condition of shells may afford some advantages to crabs with certain predators, however, crab

behaviour may be of equal or greater importance in circumventing predation. Crypsis, burrowing behaviour, or use of refugia such as seagrass beds may decrease predation by vertebrates. Birds, including especially gulls (Oldham, 1930) and fish, are effective predators on these crabs (*Pagurus*; Fig. 5). Use of weathered or fouled shells may provide camouflage for crabs in particular habitats (Blackstone, 1984; Conover, 1976; Jensen, 1970; Partridge, 1980). Fouling of shells by algae (Smyth, 1989) and hydroids (Jensen, 1970; Stachowitsch, 1980) may prevent boring organisms from weakening shells through bioerosion or may deter predators from handling shells. Abrams (1978) found strong selection against unused shells by *Coenobita compressus*, noting that crabs of this species modified the aperture as well as internal shell structures. *Coenobita compressus* in used shells chirped more often and for a longer period of time than crabs in newly liberated shells (Gilchrist, unpubl. data). Abrams also observed that a green alga coated the interior of the shell. In shell experiments with this crab species, aquatic juveniles with algae in the shell had greater numbers of shell cohabitants while adults with algae in the shells tended to have greater water retention and longer times to desiccation (Table 6).

Agonistic encounters relating to the shell resource are recorded commonly for aquatic hermit crabs. Hazlett (1966) gives a detailed description of many components to shell fighting (or shell exchange). Abrams (1982) studied shell exchange between many different species pairs in tropical and temperate zones and noted that crabs in adequate or high quality shells typically retained their shells. Further, he suggested that exploitative competition for new shells might be more important in understanding shell distribution among species than shell fighting.

Imafuku (1989) summarised 2 important features of shell fights: exchange of resource and variation in value of resource for individuals. Shell fights may include a variety of agonistic interactions. These typically include both visual and tactile components (Hazlett, 1966 *inter alia*). Field *et al.* (1987) explored the use of sound production by *Trizopagurus* as a defensive behaviour. It also aids in species recognition. In addition, they noted that the shell has only a small role in modifying the sound. *Coenobita clypeatus* and *C. compressus* sound production (chirping) may occur along with visual displays and tactile behaviour. Chirping

frequency may increase significantly when new crabs are introduced into an area (pers. obs.). *Birgus* may also use sound in such contexts (Grubb, 1971).

Male *Aratus* observed on Tidy Island in Florida may rap chelae and the fourth pereiopods on horizontal trunks when threatened by a conspecific. In tagging experiments with large male *Aratus* (carapace width >14mm), these animals exhibited a patrolling behaviour. This consisted of moving vertically on the trunk for about a half metre (either up or down), raising the chelae while tilting the front of the body outward and then zigzagging over the trunk. The same males were found on specific trees a greater amount of time than would be expected by chance alone, suggesting further studies are necessary on the potential territorial behaviour of this crab. Several similarly sized crabs occupy a tree at one time. Rarely were overt agonistic encounters observed although numerous crabs were observed with missing chelae or ambulatory appendages. These missing appendages may be explained in part by successful avoidance of predation (Table 3). In 7 cases of aggressive encounters noted in 50 hours of observation, all were on the root area of the mangrove. In each case, one crab approached the other from above. Each crab extended and raised the chelae while moving back and forth in a semicircle. The abdomen was close to the surface while the anterior of the crab was elevated. The eyestalks were lowered to about a 45° angle with the carapace. In two cases, the crabs were 'bubbling' from the oral opening. Typically, after about 90 seconds of such posturing one crab would sidestep and move away from the encounter. In 3 instances a brief shoving match followed the semicircular movements. The match ended when one crab was pushed off the surface entirely or when the first three pereiopods of one crab were lifted off the surface. The lifted crab backed away and moved around the root away from the opponent. The crab that was knocked from the surface was missing part of the left 4th pereiopod. Only male crabs were involved in 3 encounters, only females in 2 encounters, and male-female pairs were found in 2 encounters. The only other social encounters observed for these crabs were 3 probable copulatory events. The male approached a female from above and from an angle. In each case, the male then moved over the top of the female while completely surrounding her body with the pereiopods. The male then lifted his body above the female while holding the chelae

down and clasping the female with the second pereiopods. The female then gathered her appendages close to her body, and rose from the surface. After that point, copulation proceeded much the same as observed by Warner (1967). Females were hard shelled in each case.

Other forms of social encounters for *Aratus* were observed during feeding bouts around root areas of black and red mangroves. Feeding behaviour and social interactions were noted for crabs during low tide only when roots were exposed. Activity was especially noted during crepuscular low tides.

Small animals (carapace width <5mm) move to the substrate while some water is still present. Larger crabs descend when the water has receded. However, larger crabs move further and forage longer then their smaller counterparts. Crabs consumed both plant and animal material, primarily concentrating on vegetation. If red mangrove seed pods or seedlings are available, *Aratus* will be attracted to them. On seedlings, the crabs strip the leaves entirely using the chelae to remove pieces and transfer them to the mouthparts. Seeds are scraped repeatedly, dislodging them from the substrate. Larger crabs pierce the pod and tear pieces from outside. Typically only a small amount of immediate damage is done to each pod. When more then one crab converged on a seedling, the larger crab would flick the smaller crab with a chela. If crabs were nearly equal in size, the crab arriving first would elevate from the substratum and raise one or both fourth pereiopod(s). This crab would then do a series of up and down motions with the body. The approaching crab also elevated from the substrate, advancing with the chelae extended in front of the body. The first crab continued the up and down movement increasing the frequency as the second crab moved closer. Out of 17 such encounters observed, crab 1 remained at the seedling while crab 2 moved away in 11 cases; in 4 encounters crab 2 moved away; in the remaining 2 observations, a predator (*Goniopsis cruentata*) removed one of the crabs

On trees, rarely were crabs seen foraging together. Only three instances in 75 hours of observation yielded *Aratus* individuals even feeding on leaves of the same branch. Burton (1990) and Beever et al. (1976) have discussed herbivory by these crabs on mangroves in some detail.

For land hermit crabs, foraging may be subject to social facilitation. Kurta (1982) found that by orienting to aggregations of crabs, individuals increased their probability of finding food. Hazlett (1968, 1972) and Scully (1983) demonstrated that hermit crabs, observing conspecifics increasing their locomotion rate toward a food source, will likewise increase their rate of locomotion. Scully goes on to observe that large aggregations of hermit crabs may repel other organisms from a food source. During my observations on *Coenobita compressus*, rarely were large aggregations noted. The only time such groups formed were when large food items (dead bird or dead fish) were available. Typically, when feeding on the beach at the wrack line, larger crabs were solitary. Smaller crabs foraged in groups of 3–8 individuals, never straying long distances along the shoreline (one crab moved about 10 metres along the shoreline but most moved within a five metre area). Within these small groups, some flicking with pereiopods occurred occasionally.

Large groups of small crabs (>25) formed around freshwater. Crabs were observed dipping the chelae into the water and moving them to the mouthparts. As larger crabs approached, smaller crabs scattered and moved back into the jungle. Large crabs either drank in the same manner as described for the smaller crabs or immersed the entire shell into the water. Feeding and drinking behaviours of these crabs are noted elsewhere (Newton and Gilchrist, 1989). Larger crabs typically maintained a relatively large distance between each other at freshwater sources. However, clicking and chirping frequency increased as new crabs approached the water source.

Most crabs appeared to scavenge or browse for food. However, predation on both plants and animals occurred. Immature insects (grubs, caterpillars, and maggots) were readily eaten as were young leaves near the jungle floor. A wide variety of items were detected by crabs including chocolate, honey, dog food, raw eggs, and cat food.

Much like their terrestrial counterparts, marine hermit crabs may feed in aggregations of mixed sizes. It is not clear, however, whether social facilitation or chemical attraction leads to increases in aggregation size. Schembri (1982) described the feeding behaviour of fifteen species of hermit crabs from southeastern New Zealand. He found a wide range of feeding mechanisms among the group including deposit feeding, browsing, suspension feeding, predation, and scavenging. He indicated that a variety of secondary mechanisms.

During aggregate feeding, observed for marine species in Sarasota Bay, not only are conspecifics found at such sites but also other species may be attracted. *Pagurus longicarpus* was found in every mixed group. As a group forms, several types of interactions may occur. If the food item is small enough, a crab may attempt to flee with it. Typically, a tugging match ensues with each contender holding on with the major chela and plucking from the food item with the minor chela. As more crabs join, larger crabs typically displace small ones. Smaller crabs climb onto the shells of these larger crabs, collecting food from the water column above the feeding crabs. Larger crabs flick other crabs with the major chelae while holding onto the food item. If the item is too large to guard in this manner, a number of larger crabs will begin feeding on the item. Smaller crabs which try to move beneath larger crabs are typically flicked away. I have observed neither shell exchanges nor mating behaviour during such feeding bouts. Hermit crab predators are also attracted to food sources, thus shell exchanges and copulation may not be productive at feeding sites. Aggregates in marine habitats may also allow crabs to avoid predators. *Callinectes* typically approaches the aggregations from downstream, rushing the group as it nears. Fishes and birds tend to move over the groups slowly, making several quick darts before the group disband. Such predator attacks on terrestrial species have not been recorded.

SUMMARY

Clearly, terrestrialisation has led to behavioural modifications in crustaceans. Physiological differences in smaller crabs on land may serve to separate them ecologically from their adult counterparts. Physiological differences in size do not seem as important in aquatic species.

Chemical, visual, and tactile inputs are important components of modulating motivation and action of terrestrial and aquatic species. However, the relative importance of the types of cues may differ in the two media. The full extent of how chemical and acoustical information may modify behaviours is still under investigation. Further study of both the receptors and responses are necessary. In addition, careful ontogenetic studies of the morphology of receptors and development of behaviours should be completed.

LITERATURE CITED

ABELE, L.G. 1970. Semi-terrestrial shrimp (*Mergula rhizophorae*). Nature 226: 661–662

ABRAMS, P.A. 1978. Shell selection and utilization in a terrestrial hermit crab *Coenobita compressus* (M. Milne Edwards). Oecologia 34: 239–253.
1980. Resource segregation and interspecific competition in a tropical hermit crab community. Oecologia 46: 365–379.
1981. Shell fighting and competition between two hermit crab species in Panama. Oecologia 51: 84–90.
1982. Frequencies of interspecific shell exchanges between hermit crabs. Journal of Experimental Marine Biology and Ecology 61: 99–109.

BEEVER, J.W., SIMBERLOFF, D. AND KING, L.L. 1979. Herbivory and predation by the mangrove tree crab *Aratus pisonii*. Oecologia 43: 317–328.

BERTNESS, M.D. 1981. The influence of shell type on hermit crab growth rate and clutch size (Decapoda, Anomura). Crustaceana 40: 197–205.

BLACKSTONE, N. 1984. The effects of history on the shell preference of the hermit crab *Pagurus longicarpus* (Say). Journal Experimental Marine Biology Ecology 81: 225–234.

BLISS, D.E. 1968. Transition from water to land in decapod crustaceans. American Zoologist 8: 355–392.

BURGGREN, W.W. AND MCMAHON, B.R. 1988. 'Biology of land crabs', (Cambridge University Press: Cambridge). 479p.

BURTON, M. 1990. 'Levels of herbivory on black and white mangroves'. Senior thesis, New College of USF, Sarasota. 47p.

CHESSON, P.L. 1985. Coexistence of competitors in spatially and temporally varying environments: A look at the combined effects of different sorts of variability. Theoretical Population Biology 28(3): 263–287.

CONOVER, M.R. 1976. The influence of some symbionts on the shell selection behaviour of the hermit crabs, *Pagurus pollicaris* and *Pagurus longicarpus.* Animal Behaviour 24: 191–194.

DE WILDE, P.A.W.J. 1973. On the ecology of *Coenobita clypeatus* in Curacao with reference to reproduction, water economy and osmoregulation in terrestrial hermit crabs. Studies of the Fauna of Curacao 44: 1–138.

DOWDS, B.M. AND ELWOOD, R.W. 1983. Shell wars: Assessment strategies and the timing of decisions in hermit crab shell fights. Behaviour 85: 1–24.

    1985. Shell wars II: The influence of relative size on decisions made during hermit crab shell fights. Animal Behaviour 33: 649–656.

FERRIS, A. 1988. 'A biomechanical analysis of locomotion in the mangrove tree crab *Aratus pisonii*'. Senior thesis, New College of USF, Sarasota. 47p.

FIELD, L.H., EVANS, A. AND MCAMILLAN, D.L. 1987. Sound production and stridulatory structures in hermit crabs of the genus *Trizopagurus*. Journal of the Marine Biological Association of the United Kingdom 67: 89–110.

FOTHERINGHAM, N. 1980. Effect of shell utilization on reproductive patterns in tropical hermit crabs. Marine Biology 55: 287–293

GERITZ, S.A.H., METZ, J.A.J., KLINKHAMER, P.G.L., AND DEJONG, T.J. 1988. Competition in safe-sites. Theoretical Population Biology 33(2): 161–180.

GHERARDI, F. AND VANNINI, M. 1989. Field observations on activity and clustering in two intertidal hermit crabs, *Clibanarius virescens* and *Calcinus laevimanus* (Decapoda, Anomura). Marine Behaviour and Physiology 14: 145–159.

GHIRADELLA, H.T., CASE, J.F. AND CRANSHAW, J. 1968. Structure of aesthetascs in selected marine and terrestrial decapods: chemoreceptor morphology and environment. American Zoologist 8: 603–621.

GIBSON-HILL, C.A. 1947. Field notes on terrestrial crabs. Bulletin of Raffles Museum 18: 43–52.

GILCHRIST, S. 1982. 'A critical view of hermit crab shell use'. PhD Dissertation. Florida State University, Tallahassee, Florida, USA. 137p.

GILCHRIST, S., SCOTTO, L. AND GORE, R.H. 1983. Early zoeal stages of the semiterrestrial shrimp *Merguia rhizophorae* (Rathbun, 1900) cultured under laboratory conditions (Decapoda, Natantia, Hippolytidae) with a discussion of characters in the larval genus *Eretmocaris*. Crustaceana 45(3): 238–259.

GILCHRIST, S. AND ABELE, L.G. 1984. Effects of sampling method on the estimation of population parameters in hermit crabs. Journal of Crustacean Biology 4: 645–654.

GRUBB, P. 1971. Ecology of terrestrial decapod crustaceans on Aldabra. Philosophical Transaction of the Royal Society of London, Series B 260: 411–416.

HAZLETT, B.A. 1966. Social behaviour of the Paguridae and Diogenidae of Curacao. Studies of the Fauna of Curacao and other Caribbean Islands 23: 1–143.

    1968. Stimuli involved in feeding behaviour of the hermit crab *Clibanarius vittatus*. Zeitschrift für Tierpsychologie 25: 608–614.

    1970. Tactile stimuli in the social behaviour of *Pagurus bernhardus* (Decapoda, Paguridae). Behaviour 36: 20–40.

    1972. Ritualization in marine crustacea. 97–125. In H.E. Winn and B.L. Olla (eds) 'Behaviour of marine animals, vol. 1, Invertebrates'. (Plenum Press: New York).

    1978. Shell exchanges in hermit crabs: aggression, negotiation, or both. Animal Behaviour 26: 1278–1279.

    1981. Influence of rearing conditions on initial shell entering behaviour of a hermit crab (Decapoda, Paguridae). Crustaceana 20(2): 167–170.

    1983. Interspecific negotiation: mutual gain in exchanges of a limiting resource. Animal Behaviour 31: 160–163.

    1989. Mating success of male hermit crabs in shell generalist and shell specialist species. Behavioural Ecology and Sociobiology 25: 119–128.

HAZLETT, B.A. AND BARON, L.C. 1989. Influence of shells on mating behaviour in the hermit crab *Calcinus tibicen*. Behavioural Ecology and Sociobiology 24: 369–376.

HAZLETT, B.A. AND ESTABROOK, G. 1974. Examination of agonistic behaviour by character analysis. II Hermit crabs. Behaviour 49: 88–110.

HELFMAN, G.S. 1979. Coconut crabs and cannibalism. Natural History 88: 76–83.

HERREID II, C.F. AND FULL, R.J. 1986. Locomotion of hermit crabs (*Coenobita compressus*) on beach and treadmill. Journal of Experimental Biology 120: 283–296.

IMAFUKU, M. 1986. Sexual discrimination in the hermit crab *Pagurus geminus*. Journal of Ethology 4: 39–47.

    1989. Shell fights in the hermit crab *Pagurus geminus*: Effect of cheliped use and shell rapping. Journal of Ethology 7: 35–39.

IMAFUKU, M. AND IKEDA, H. 1990. Sound production in the land hermit crab *Coenobita pur-*

purcus Stimpson, 1958 (Decapoda, Coeno-bitidae). Crustaceana 58(2): 168–174.

JENSEN, K. 1970. The interaction between *Pagurus bernhardus* (L.) and *Hydractinia echinata* (Fleming). Ophelia 8: 135–144.

KELLOGG, C.W. 1976. Gastropod shells: A potentially limiting resource for hermit crabs. Journal of Experimental Marine Biology and Ecology 22: 101–111.

KINOSITA, H. AND OKAJIMA, A. 1968. Analysis of shell searching behaviour of the land hermit crab *Coenobita rugosus* H. Milne Edwards. Journal Faculty Science Tokyo 11: 293–358.

KURTA, A. 1982. Social facilitation of foraging behaviour by the hermit crab, *Coenobita compressus*, in Costa Rica. Biotropica 14: 132–136.

LEPORE, M. AND GILCHRIST, S. 1988. Hermit crab attraction to gastropod predation sites. American Zoologist 28(4): 72A.

MCLEAN, R.B. 1974. Direct shell acquisition by hermit crabs from gastropods. Experientia 30: 206–208.

MCMAHON, B.R. AND BURGGREN, W.W. 1981. Acid-base balance following temperature acclimation in land crabs. Journal of Experimental Zoology 218: 45–52.

MORRIS, S., GREENAWAY, P., AND MCMAHON, B.R. 1988. Adaptations to a terrestrial existence by the robber crab *Birgus latro*: I. An *in vitro* investigation of blood gas transport. Journal of Experimental Biology 140: 477–491.

NEIL, S.J. AND ELWOOD, R.W. 1985. Behavioural modifications during egg-brooding in the hermit crab, *Pagurus bernhardus* L. Journal of Experimental Marine Biology and Ecology 94: 99–114.

NEWTON, N. AND GILCHRIST, S. 1989. Feeding and shell preferences of terrestrial hermit crabs. American Zoologist 29(4): 37A.

OLDHAM, C. 1930. The shell smashing habits of gulls. Ibis 6: 239–244.

PARTRIDGE, B.L. 1980. Background camouflage: An additional parameter in hermit crab shell selection and subsequent behaviour. Bulletin of Marine Science 30(4): 914–916.

PAGE, H.M. AND WILLASON, S.W. 1982. Distribution patterns of terrestrial hermit crabs at Enewetak Atoll, Marshall Islands. Pacific Science 36(1): 107–117.

REBACH, S. AND DUNHAM, D. 1983. 'Studies in adaptation: The behaviour of higher Crustacea' (John Wiley and Sons Inc.: New York). 282p.

REESE, E.S. 1963. The behavioural mechanisms underlying shell selection by hermit crabs. Behaviour 21: 78–126.

RITTSCHOF, D. 1980. Chemical attraction of hermit crabs and other attendants to simulated gastropod predation sites. Journal of Chemical Ecology 6: 103–118.

RITTSCHOF, D. AND SUTHERLAND, J.P. 1986. Field studies on chemically mediated behaviour in land hermit crabs: Volatile and nonvolatile ordors. Journal of Chemical Ecology 12(6): 1273–1284.

SCULLY, E.P. 1983. The behavioural ecology of competition and resource utilization among hermit crabs.23–55. In S. Rebach and D. Dunham (eds) 'Studies in adaptation: The behaviour of higher Crustacea'. (John Wiley and Sons Inc.: New York).

SCHEMBRI, P.J. 1982. Feeding behaviour of fifteen species of hermit crabs (Crustacea: Decapoda: Anomura) from the Otago region, southeastern New Zealand. Journal of Natural History 16: 859–878.

SEIPLE, M. AND SALMON, W. 1982. Comparative social behaviour of two grapsid crabs, *Sesarma reticulatum* (Say) and *S. cinereum* (Bosc). Journal of Marine Biology and Ecology 62: 1–24.

SMYTH, M.J. 1989. Bioerosion of gastropod shells: with emphasis on effects of coralline algae cover and shell microstructure. Coral Reefs 8: 119–125.

SNYDER-CONN, E. 1980. Tidal clustering and dispersal of the hermit crab *Clibanarius digueti*. Marine Behaviour and Physiology 7: 135–154.
1981. The adaptive significance of clustering in the hermit crab *Clibanarius digueti*. Marine Behaviour and Physiology 8: 43–53.

SPIGHT, T. 1977. Availability and use of shells by intertidal hermit crabs. Biological Bulletin of the Marine Biology Laboratory, Woods Hole 152: 120–133.

STACHOWITSCH, M. 1980. The epibiotic and endolithic species associated with gastropod shells inhabited by hermit crabs *Paguristes oculatus* and *Pagurus cuanensis*. Marine Ecology 1: 73–101.

TAYLOR, P. 1981. Hermit crab fitness: The effect of shell condition and behavioural adaptations on environmental resistance. Journal Marine Biology Ecology 52: 205–218.

TAYLOR, P.D., SCHEMBRI, P.J. AND COOK, P.L. 1989. Symbiotic associations between hermit crabs and bryozoans from the Otago region, southeastern New Zealand. Journal of Natural History 23: 1059–1085.

TAYLOR, R.C. 1967a. The anatomy and adequate stimulation of a chordotonal organ in the

antennae of a hermit crab. Comparative Biochemistry and Physiology 20: 709–717.

1967b. Functional properties of the chordotonal organ in the antennal flagellum of a hermit crab. Comparative Biochemistry and Physiology 20: 719–729.

VANCE, R.R. 1972. Competition and mechanism of coexistence in three sympatric species of intertidal hermit crabs. Ecology 53: 1063–1074.

WARNER, G.F. 1967. The life history of the mangrove tree crab, *Aratus pisonii*. Journal of Zoology (London) 153: 321–335.

WILBER, JR., T.P. AND HERRNKIND, W.F. 1982. Rate of new shell acquisition by hermit crabs in a salt marsh habitat. Journal of Crustacean Biology 2: 588–592.

WILSON, K.A. 1985. 'Physical and biological interactions that influence habitat use of mangrove crabs'. PhD dissertation, University of Pennsylvania. 167p.

WOLCOTT, T. 1988. Ecology. 55–96. In W.W. Burggren and B.R. McMahon (eds) 'Biology of the land crabs'. (Cambridge University Press: Cambridge).